



The Brazil Eucalyptus Potential Productivity Project: Influence of water, nutrients and stand uniformity on wood production

Jose Luiz Stape^{a,*}, Dan Binkley^b, Michael G. Ryan^{c,d}, Sebastiao Fonseca^e, Rodolfo A. Loos^e, Ernesto N. Takahashi^e, Claudio R. Silva^e, Sergio R. Silva^f, Rodrigo E. Hakamada^f, Jose Mario de A. Ferreira^g, Augusto M.N. Lima^g, Jose Luiz Gava^h, Fernando P. Leiteⁱ, Helder B. Andrade^j, Jacyr M. Alves^k, Gualter G.C. Silva^l, Moises R. Azevedo^m

^a Department Forestry and Environmental Resources, North Carolina State University, Raleigh, NC 27695, USA

^b Warner College of Natural Resources, Colorado State University, Fort Collins, CO 80523, USA

^c Rocky Mountain Research Station, USDA Forest Service, 240 W. Prospect, Fort Collins, CO 80526, USA

^d Affiliate Faculty, Graduate Degree Program in Ecology, Colorado State University, Fort Collins, CO 80523, USA

^e Fibria Celulose, Aracruz, Espirito Santo, Brazil

^f Veracel Celulose, Eunapolis, Bahia, Brazil

^g International Paper do Brasil, Mogi Guacu, Sao Paulo, Brazil

^h Suzano Papel e Celulose, Teixeira de Freitas, Bahia, Brazil

ⁱ CENIBRA, Ipatinga, Minas Gerais, Brazil

^j Vallourec-Mannesmann, Bocaiuva, Minas Gerais, Brazil

^k Copener Florestal, Alagoinhas, Bahia, Brazil

^l Universidade Federal do Rio Grande do Norte, Natal, Mossoro, Rio Grande do Norte, Brazil

^m Universidade Federal da Bahia, Salvador, BA, Brazil

ARTICLE INFO

Article history:

Received 20 October 2009

Received in revised form 2 January 2010

Accepted 10 January 2010

Keywords:

Eucalyptus production

Forest irrigation

Age-related decline

Geographic gradient

Tropical plantation silviculture

ABSTRACT

We examined the potential growth of clonal Eucalyptus plantations at eight locations across a 1000+ km gradient in Brazil by manipulating the supplies of nutrients and water, and altering the uniformity of tree sizes within plots. With no fertilization or irrigation, mean annual increments of stem wood were about 28% lower ($16.2 \text{ Mg ha}^{-1} \text{ yr}^{-1}$, about $33 \text{ m}^3 \text{ ha}^{-1} \text{ yr}^{-1}$) than yields achieved with current operational rates of fertilization ($22.6 \text{ Mg ha}^{-1} \text{ yr}^{-1}$, about $46 \text{ m}^3 \text{ ha}^{-1} \text{ yr}^{-1}$). Fertilization beyond current operational rates did not increase growth, whereas irrigation raised growth by about 30% (to $30.6 \text{ Mg ha}^{-1} \text{ yr}^{-1}$, about $62 \text{ m}^3 \text{ ha}^{-1} \text{ yr}^{-1}$). The potential biological productivity (current annual increment) of the plantations was about one-third greater than these values, if based only on the period after achieving full canopies. The biological potential productivity was even greater if based only on the full-canopy period during the wet season, indicating that the maximum biological productivity across the sites (with irrigation, during the wet season) would be about $42 \text{ Mg ha}^{-1} \text{ yr}^{-1}$ ($83 \text{ m}^3 \text{ ha}^{-1} \text{ yr}^{-1}$). Stands with uniform structure (trees in plots planted in a single day) showed 13% greater growth than stands with higher heterogeneity of tree sizes (owing to a staggered planting time of up to 80 days). Higher water supply increased growth and also delayed by about 1 year the point where current annual increment and mean annual increment intersected, indicating opportunities for lengthening rotations for more productive treatments as well as the influence of year-to-year climate variations on optimal rotations periods. The growth response to treatments after canopy closure (mid-rotation) related well with full-rotation responses, offering an early opportunity for estimating whole-rotation yields. These results underscore the importance of resource supply, the efficiency of resource use, and stand uniformity in setting the bounds for productivity, and provide a baseline for evaluating the productivity achieved in operational plantations. The BEPP Project showed that water supply is the key resource determining levels of plantation productivity in Brazil. Future collaboration between scientists working on silviculture and genetics should lead to new insights on the mechanisms connecting water and growth, leading to improved matching of sites, clones, and silviculture.

© 2010 Elsevier B.V. All rights reserved.

* Corresponding author.

E-mail address: jlstape@ncsu.edu (J.L. Stape).

1. Introduction

Eucalyptus plantations in Brazil in 1970 typically grew at rates of about $15 \text{ m}^3 \text{ ha}^{-1} \text{ yr}^{-1}$ (Queiroz and Barrichelo, 2008). Over the next 35 years, intensive research and improved operations tripled the average yields across almost 4 million ha, through improved silviculture (site preparation, fertilization and control of leaf-cutting ants and weeds), improved seed selection, and the development of clonal propagation (Goncalves et al., 2008). Empirical analysis of growth responses in experimental plantations guided management decisions, but the ecophysiological factors behind these empirical patterns remained largely unexamined until the late 1990s (Almeida et al., 2004; Stape et al., 2004a,b; Whitehead and Beadle, 2004). To what extent is forest growth limited by environmental constraints (such as incoming light and vapor pressure deficit), by the supplies of nutrients and water, and by inadequate silvicultural practices?

The Brazil Eucalyptus Potential Productivity (BEPP) Project was launched in 2001 to determine potential growth rates when nutrient and water limitations are removed across a geographic range of sites and clones, including the processes behind the responses in wood growth (carbon allocation, resource use and efficiency). As part of this special issue on Productivity in Tropical Plantations, this paper provides an overview of the BEPP Project, summarizes the basic patterns of stand growth, and tests a hypothesis that age-related decline in growth increases with increasing heterogeneity of tree sizes within stands. Other papers in this special issue examine carbon budgets (Ryan et al., 2010), patterns of resource use efficiency by individual trees (Binkley et al., 2010), and water use (Hubbard et al., 2010) in the BEPP Project.

The initial ideas tested in the BEPP Project developed from an earlier research project on age-related decline in a *Eucalyptus saligna* plantation in Hawaii (Ryan et al., 2004). Wood growth and gross primary production declined substantially after mid-rotation in that study, despite the high supply of water and repeated fertilization. A decline in photosynthesis was the largest contributor to the decline in wood production, with smaller contributions from increased partitioning to belowground and foliar respiration. The growth decline was traced to a loss of efficiency of production per unit of resource used, rather than to a decline in resource use. Dominant trees showed higher efficiency of resource use (Binkley et al., 2002), leading to hypotheses about changes in dominance and resource use efficiency as drivers of age-related decline (Binkley, 2004).

A pilot experiment for the BEPP Project tested the effects of irrigation and fertilization on maximum growth rates in a single plantation by Copener Florestal near Alagoinhas, Bahia (Stape et al., 2008). The results from this individual site were designed to be extrapolated to a broader landscape in Bahia with two approaches. Local parameterization of the 3-PG forest growth model (Landsberg and Waring, 1997) provided an opportunity for estimating growth for different soils and environments in the region (Stape et al., 2004a), and an empirical approach to extrapolation was developed with a “twin-plot” approach that joined routine forest inventory plots with simple stand treatments (Stape et al., 2004b).

The BEPP Project developed as a consortium of eight companies, the University of São Paulo, Colorado State University, and the USDA Forest Service, coordinated through the Forestry Science and Research Institute (IPEF) in Brazil. Each company installed a basic version of the potential productivity experiment (testing irrigation and repeated fertilization). Routine measurements of stem growth were supplemented with regular sampling of canopy leaf area, belowground carbon flux, and other features needed for production ecology insights. The companies were responsible for routine measurements, with training assistance from other BEPP collaborators.



Fig. 1. Location of the 8 BEPP sites (site codes in Table 1).

2. Methods

2.1. Sites

The BEPP sites spanned a distance of more than 1000 km in southeastern Brazil (Fig. 1). The environmental gradients included three Soil Orders, a three-fold range in soil clay percent, and a 70% range in rainfall (Tables 1 and 2). The sites ranged from warm tropical with low vapor pressure deficits to subtropical environments and large vapor pressure deficits. This paper analyzes patterns for a full-rotation of 6 years for three sites (ARA, IPB, and VER); 4–5 years of stand development were available for 4 other sites (CEN, SUZ, VIP and VLM), and just 3 years of development were obtained for an 8th site (VCP) before a severe windstorm stopped the experiment. The damage was notably greater in the irrigated treatments than in the non-irrigated treatments, underscoring a higher risk of wind damage for rapidly growing, large canopy trees. Prior land use included previous rotations of Eucalyptus plantations, except for the VER site (former grassland) and IPB site (orange orchard).

2.2. Treatments

The potential productivity (for each set of site and clone) was determined at all locations based on typical current silvicultural operations as the baseline treatment for comparison. These baseline treatments all included the use of clonal plantlets (chosen by each company, Table 1), operational levels of fertilization (Table 3), and sustained weed control. Plot size was $30 \text{ m} \times 30 \text{ m}$, with tree spacing near $3 \text{ m} \times 3 \text{ m}$. With two rows of buffer trees, the interior measurement subplots had 6 rows and 6 columns of trees. Irrigation treatments were tested at all sites (Table 4) to remove any limitation of soil water supply on growth (trenching between plots minimized any influence of adjacent treatments, Fig. 2). Rates of irrigation were tailored at each site to supplement rainfall and exceed potential evapotranspiration each week, with an average 15–30 mm applied twice weekly. Current operational rates of fertilization may not completely alleviate nutrient limitation, so all sites included a high fertilization treatment with fertilizer applications three times annually for the first 3 years (with rates varying among companies, Table 3).

Table 1
Site and plantation descriptions. Soil attributes for a depth of 0–40 cm.

Site code, location	Latitude (S), longitude (W)	Elevation (m)	Soil order	pH (0.1 M CaCl ₂)	Sum base cations (mmol _c kg ⁻¹)	Clay (%)	Genetic clone	Planting date
ARA—Aracruz, ES	19°49', 40°05'	12	Ultisol	4.0	23	37	3918	March 2001
CEN—Guanhaes, MG	18°35', 42°59'	870	Oxisol	4.0	21	65	57, 1213, 7074, 386	April 2004
IPB—Mogi Guacu, SP	22°21', 46°58'	312	Oxisol	6.0	75	45	13	October 2000
SUZ—Teixeira de Freitas, BA	18°02', 39°52'	84	Ultisol	4.4	27	21	10	December 2001
VCP—Luis Antonio, SP	21°32', 48°22'	680	Entisol	3.9	8	28	37	March 2000
VER—Eunapolis, BA	16°21', 39°34'	187	Ultisol	4.3	35	37	53	March 2001
VIP—Luis Antonio, SP	21°32', 48°22'	680	Entisol	3.9	12	28	41	August 2003
VLM—Bocaiuva, MG	17°20', 43°50'	900	Oxisol	5.5	42	48	1, 3, 4, 463	February 2005

Table 2
Climate characteristics for the sites (site codes in Table 1). Values are annual averages across years, measured or estimated at each site. Values for the wet season are October to March, those for the dry season are April to September. Potential evapotranspiration based on equations from Thornthwaite and Mather (1957).

	ARA	CEN	IPB	SUZ	VCP	VER	VIP	VLM
Average temperature (°C)	23.6	19.4	21.6	23.1	22.0	23.0	22.7	23.6
(Dry season; wet season)	(22.3; 24.9)	(18.3; 20.6)	(19.6; 23.2)	(20.4; 25.1)	(20.8; 24.2)	(21.3; 24.5)	(21.8; 23.6)	(20.5; 25.0)
PAR (MJ m ⁻² yr ⁻¹)	2752	2555	3055	2921	3063	3114	2949	3474
(Dry season; wet Season)	(1184; 1568)	(1150; 1405)	(1375; 1680)	(1286; 1635)	(1348; 1715)	(1339; 1775)	(1445; 1504)	(1772; 1702)
Vapor pressure deficit (kPa)	0.78	0.63	1.05	0.76	1.06	0.78	1.05	1.30
Rainfall (mm yr ⁻¹)	1360	1108	1317	1351	1307	1433	1247	848
(Dry season, wet season)	(490; 870)	(188; 920)	(250; 1067)	(446; 905)	(235; 1072)	(545; 888)	(200; 1047)	(76; 772)
Irrigation water (mm yr ⁻¹)	701	1116	796	1715	1045	846	440	1554
Total water for irrigated treatment (mm yr ⁻¹)	2061	2224	2113	3066	2352	2279	1687	2402
Potential evapotranspiration (mm yr ⁻¹)	1204	876	1024	1255	1087	1144	1124	1221

Table 3
Total fertilization amounts added (kg of element per hectare) through the end of the rotation, or to the last measurement in 2009 (see site codes in Table 1). The F treatment also received other micronutrients.

SITE	Treatment (T = traditional, F = high fertilization)	Nitrogen	Phosphorus	Potassium	Calcium	Magnesium	Boron
ARA	F	967	374	753	634	40	6
	T	77	54	89	585	40	1
SUZ	F	510	219	409	229	–	5
	T	52	44	66	112	–	2
CEN	F	732	145	570	918	180	8
	T	86	40	171	705	120	3
IPB	F	640	238	498	996	180	5
	T	33	44	27	–	–	2
VLM	F	444	160	369	280	60	8
	T	79	55	66	280	60	6
VER	F	1012	374	797	1074	180	5
	T	12	46	18	62	–	–
VIP	F	594	240	546	620	120	2
	T	21	33	136	396	72	2
VCP	F	724	284	669	776	60	–
	T	14	14	109	240	24	–

Table 4
Production ecology treatments applied at each site (see Table 1 for site codes). Three-letter treatment codes (in bold) denote nutrient treatment, water treatment, and stand structure treatment.

	Uniform stand structure (U)			Heterogeneous stand structure (H)	
	No fertilization (control)	Traditional fertilization (T)	High fertilization (F)	Traditional fertilization (T)	High fertilization (F)
Not irrigated (N)	Code CNU: CEN, VCP, VIP	Code TNU: ARA, CEN, IPB, SUZ, VCP, VER, VIP, VLM	Code FNU: ARA, CEN, IPB, SUZ, VCP, VER, VIP, VLM	Code TNH: IPB, SUZ, VER	
Irrigated (I)		Code TIU: CEN, IPB, VCP, VER, VIP, VLM	Code FIU: ARA, CEN, IPB, SUZ, VCP, VER, VIP, VLM	Code FIH: ARA, IPB, SUZ, VCP, VER	



Fig. 2. Upper: Aerial photograph of one of the BEPP site (IPB), at Mogi Guacu, SP at 4 months old (with lines traced on the photo to show plot boundaries). Notice the uniform plots and the heterogeneous plots developing in response to staggered planting times within plots. Lower: Boundary (and trench) between uniform (left) and heterogeneous (right) treatment at the IPB site at 2.5 years.

The influence of stand structure was examined at four sites, with uniform plots (planted with clonal trees in a single day) and heterogeneous plots. Heterogeneity developed by staggering the day of planting within a plot (design suggested by Christian Giardina), with one-third of points planted on Day 0, one-third on Day 40, and one-third on Day 80. The selection of planting points was random for a given day, providing a continuous distribution of tree sizes that mimicked seedling-origin stands (Boyden et al., 2008; Binkley et al., 2010).

2.3. Measurements of tree mass and growth

Tree diameters and heights were measured every 3 months. Biomass regressions equations were developed separately for each site based on destructive harvesting (in spare plots) at about 1.5, 3, and 6 years. Stem wood mass correlated very highly with tree diameter and height for all sites and treatments (r^2 greater than 0.98):

$$\begin{aligned} \text{ARA: Mass} &= 0.0040 \times D^{1.959} \times H^{1.512} \quad (n = 128) \\ \text{CEN: Mass} &= 0.0260 \times D^{1.174} \times H^{1.503} \quad (n = 53) \\ \text{IPB: Mass} &= 0.0050 \times D^{1.751} \times H^{1.542} \quad (n = 169) \\ \text{SUZ: Mass} &= 0.0090 \times D^{1.622} \times H^{1.515} \quad (n = 92) \\ \text{VCP: Mass} &= 0.0170 \times D^{2.596} \times H^{0.427} \quad (n = 44) \\ \text{VER: Mass} &= 0.0270 \times D^{2.221} \times H^{0.625} \quad (n = 264) \\ \text{VIP: Mass} &= 0.0003 \times D^{1.592} \times H^{1.712} \quad (n = 36) \\ \text{VLM: Mass} &= 0.0080 \times D^{1.778} \times H^{1.497} \quad (n = 35) \end{aligned}$$

where Mass is stemwood mass (kg), D diameter (cm) at 1.3 m height, H (m) total tree height, and n is the number of trees used in each equation.

2.4. Statistical analysis

Within each site, the experiment was a completely randomized block design with four replicate plots (3 for ARA). Two levels of statistical inference were examined. The replication within each site provided for a population of inference of a few hectares, over the time span (and weather patterns) of the measurement periods. The results from individual locations (analyzed by analysis of variance for the within-site effects of fertilization, irrigation, and stand structure, including main effects and interactions) would probably provide reliable insights for plantations on similar soils in nearby areas. The primary focus of this paper is the treatment response across all sites, so the second level of inference used the average results from each treatment at a site as a unit of observation (examined by analysis of variance for the among-site effects of fertilization, irrigation, and stand structure, including main effects and interactions), and the population of inference would be a large portion of the Eucalyptus plantations across southeastern Brazil. Correlations were used to relate stem diameter and height to mass; to examine patterns between stand values and site factors; and to characterize some patterns in stand growth at different time periods. All analyses were performed with SAS 8.2 (SAS Institute, 2000), using a P value of 0.05 for evaluating the likely significance of treatment effects. Although prior expectations would have justified the use of one-tailed statistical tests for some hypotheses (for example, that irrigation would increase growth), we nonetheless used only two-tailed tests to provide a consistent, conservative set of hypothesis tests. No transformations were needed to meet ANOVA assumptions.

3. Results

Survival was very high across all treatments and sites, providing fully stocked plots (Table 5) for evaluating the effects of treatments. The one exception was the VCP site that was abandoned after 2.8 years following major breakage of trees in a severe windstorm (up to 1/3 of trees damaged in irrigated plots, with almost no damage in non-irrigated plots). The site index for the baseline treatment of traditional fertilization without irrigation (TNU) ranged from 25 to 32 m at 5 years (Table 5), corresponding with mean annual increments of 18–30 Mg ha⁻¹ yr⁻¹ (Table 6; about 37–62 m³ ha⁻¹ yr⁻¹).

3.1. Fertilization response

All treatments influenced growth fairly consistently, from the time of plantation establishment through the final measurement (Fig. 3). The CNU treatment (no fertilization, no irrigation, uniform structure) was tested at three sites, and led to a 28% reduction in mean annual increment (MAI) relative to the baseline TNU treatment (Fig. 4, Table 6). The effect was significant at the VIP and VCP sites, but not at the CEN site; across all three sites, the P -value for this treatment was 0.10 (or 0.05 for a one-tailed hypothesis test (that CNU would grow less than TNU)). Increasing fertilization rates from current operational levels (TNU) to very high rates (FNU) had no significant effect on growth within any site, or across all sites together. Fertilization showed no significant interactions with irrigation or stand structure.

3.2. Irrigation response

The response to irrigation was far larger than fertilization (comparing all non-irrigated and irrigate treatments), with MAI increasing by an average of 30%. The irrigation effect was significant within all sites except for the CEN site ($P = 0.28$). The growth increase from irrigation ranged from a low of 7% (1.7 Mg ha⁻¹ yr⁻¹, not

Table 5

Tree and stand values by treatment and site at the end-of-rotation or last measurement in 2009; site codes from Table 1 treatment codes from Table 4. Values are means with standard errors of the means in parentheses ($n=4$ for all sites (3 for ARA)). For each site and variable, values followed by different letters differ at $P=0.05$.

Site age (years)	Stocking (tree ha ⁻¹)	DBH (cm)	Height (m)	Site index (m, 5 years)	Basal area (m ² ha ⁻¹)	Wood (Mg ha ⁻¹)	MAI (Mg ha ⁻¹ yr ⁻¹)
ARA (6.0 years)							
TNU	1100 (17) a	14.9 (0.4) b	22.7 (0.2) ab	25.2 (0.4) b	20.1 (1.2) c	109.9 (5.3) c	18.3 c
FNU	1100 (17) a	15.0 (0.3) b	22.8 (1.4) ab	26.3 (1.4) a	20.4 (0.7) c	115.1 (12.0) c	19.2 c
FIU	1111 (0) a	16.7 (0.6) a	24.4 (1.1) a	27.3 (0.7) a	26.2 (1.5) a	169.1 (13.3) a	28.2 a
FIH	1069 (17) b	15.2 (0.8) b	21.1 (1.1) b	28.1 (0.4) a	22.9 (1.6) b	144.5 (14.8) b	24.1 b
IPB (6.0 years)							
TNU	1153 (42)	17.0 (0.4) c	27.9 (0.5) b	29.9 (0.6) d	27.2 (1.9) c	153.8 (13.8) d	25.6 d
FNU	1161 (101)	17.2 (0.6) c	28.0 (0.6) b	29.8 (0.6) cd	28.1 (1.6) b	159.4 (12.5) c	26.6 c
TIU	1186 (17)	18.8 (0.9) a	29.1 (1.0) a	31.4 (0.3) ab	34.4 (2.6) a	205.8 (18.5) a	34.3 a
FIU	1161 (43)	18.2 (0.6) b	27.8 (1.4) b	31.4 (0.4) ab	32.5 (2.9) a	190.6 (20.5) b	31.8 b
TNH	1085 (84)	16.2 (0.3) d	26.0 (0.1) c	29.9 (0.4) bc	24.7 (0.8) d	137.2 (5.1) e	22.9 e
FIH	1136 (42)	17.2 (0.4) c	25.8 (0.6) c	31.5 (0.3) a	30.0 (1.2) b	173.0 (8.0) c	28.8 c
VER (6.0 years)							
TNU	1087 (29) a	18.8 (0.8) b	30.9 (0.6) bc	32.0 (0.9) c	31.1 (2.3) ab	178.7 (18) bc	29.8 bc
FNU	1064 (31) a	19.4 (1.9) ab	31.0 (1.7) bc	32.8 (1.3) bc	32.5 (6.8) ab	190.5 (49.9) ab	31.8 ab
TIU	1072 (29) a	20.5 (0.4) a	32.6 (0.6) a	33.6 (0.9) ab	36.3 (2.5) a	220.2 (16) a	36.7 a
FIU	1080 (25) a	20.3 (0.4) a	32.1 (0.3) ab	33.4 (0.8) bc	35.9 (2.1) a	214.8 (12.7) a	35.8 a
TNH	1103 (15) a	16.0 (1.3) c	26.9 (0.8) d	32.5 (1.4) bc	25.3 (4.4) c	144.4 (31.2) c	24.1 c
FIH	918 (81) b	19.3 (0.4) ab	29.9 (0.9) c	33.6 (0.5) a	29.1 (2.4) bc	176.6 (12.9) bc	29.4 bc
SUZ (5.5 years)							
TNU	1111 (0) a	15.2 (0.3) b	25.7 (0.5) b	27.1 (0.9) b	20.6 (0.8) b	117.8 (5.2) b	21.4 b
FNU	1087 (15) ab	15.5 (0.1) b	25.8 (0.1) b	26.3 (0.2) b	20.9 (0.6) b	118.7 (3.4) b	21.6 b
FIU	1041 (58) bc	17.0 (0.4) a	27.0 (1.0) a	29.4 (0.5) a	24.4 (0.8) a	145.3 (4.2) a	26.4 a
TNH	1087 (29) ab	14.5 (0.2) c	24.4 (0.4) c	27.0 (0.2) b	18.9 (0.7) c	103.9 (4.8) c	18.9 c
FIH	1018 (56) c	16.8 (0.5) a	26.2 (1.1) a	29.6 (0.8) a	23.7 (0.5) a	138.2 (8.6) a	25.1 a
CEN (5.3 years)							
CNU	1111 (0)	16.8 (1.1) c	26.0 (2.2) b	28.4 (1.3) b	25.5 (3.3) b	111.9 (19.2) b	21.3 b
TNU	1095 (31)	17.8 (1.3) b	27.5 (2.9) ab	29.3 (2.7) a	27.9 (3.3) ab	127.3 (24.8) ab	24.3 ab
FNU	1111 (0)	18.1 (1) b	27.3 (2.7) ab	29.8 (2.1) a	29.5 (3.5) a	131.0 (22.6) ab	25.0 ab
TIU	1095 (31)	18.7 (1) a	27.7 (2.7) a	30.5 (0.7) a	31.2 (3.7) a	138.9 (24.8) a	26.5 a
FIU	1041 (139)	19 (1.3) a	28.3 (2.2) a	30.8 (1.0) a	30.8 (6.9) a	137.6 (29.7) a	26.2 a
VIP (4.8 years)							
CNU	1318 (25) a	12.3 (0.9) d	21.6 (2.2) c	26.0 (2.0) c	16.6 (2.8) d	68.7 (25.1) c	14.5 c
TNU	1210 (22) b	15.3 (0.4) c	24.4 (1.2) ab	28.6 (0.7) b	23.3 (1.2) c	114.1 (15.0) b	24.0 b
FNU	1266 (76) ab	15.4 (1.0) c	23.0 (3.2) bc	29.0 (1.1) b	24.9 (2.4) c	114.1 (31.2) b	24.0 b
TIU	1310 (25) ab	16.5 (0.3) b	24.7 (1.5) ab	30.8 (0.8) a	30.0 (1.0) a	150.7 (18.8) a	31.7 a
FIU	1088 (92) c	17.3 (0.9) a	25.0 (1.9) a	31.3 (0.5) a	27.6 (3.4) b	133.3 (35.3) a	28.1 a
VLM (4.5 years)							
TNU	1018 (185)	14.3 (0.7) b	21.6 (1.7) b	26.5 (1.4) c	16.3 (1.6) c	93.7 (12.2) b	20.8 b
FNU	1080 (62)	14.5 (0.6) b	22.1 (2) b	28.0 (2.0) b	18.2 (1.1) b	108.1 (18.5) b	24.0 b
TIU	1056 (108)	17.2 (0.4) a	24.8 (1.9) a	30.0 (1.6) a	24.8 (2.1) a	168.1 (24.2) a	37.4 a
FIU	1056 (89)	17.3 (0.5) a	24.9 (1.8) a	30.8 (2.2) a	25.1 (1.5) a	171.0 (21.0) a	38.0 a
VCP (2.8 years)							
CNU	966 (170) ab	11.1 (0.9) c	17.2 (0.9) c	26.0 (1.1) b	9.7 (1.3) d	31.2 (5.3) d	11.4 d
TNU	1041 (52) a	12.4 (0.1) b	18.3 (0.5) b	26.8 (0.7) b	12.8 (0.4) c	43.7 (0.9) c	15.9 c
FNU	1056 (68) a	12.5 (0.2) b	18.0 (0.5) b	26.4 (0.8) b	13.2 (0.5) c	45.2 (2.3) c	16.5 c
TIU	948 (29) ab	14.2 (0.2) a	20.0 (0.7) a	29.2 (0.5) a	15.4 (0.4) b	59.7 (2.7) b	21.7 b
FIU	1080 (35) a	14.3 (0.3) a	20.2 (0.7) a	29.9 (0.5) a	17.7 (0.4) a	69.8 (3.0) a	25.4 a
FIH	894 (90) b	14.5 (0.3) a	19.5 (0.2) a	29.5 (0.6) a	15.2 (0.7) b	60.3 (2.4) b	22.0 b

significant) at the cooler, higher elevation CEN site to 67% (15.2 Mg ha⁻¹ yr⁻¹) at the driest VLM site. Irrigation did not show a significant interaction with stand structure.

The magnitude of the irrigation response related well to some of the climate parameters, with stronger relationships when the response was gauged in units of Mg ha⁻¹ yr⁻¹ than as percent. The strongest relationships occurred between irrigation response and non-irrigated water balance (rainfall minus potential evapotranspiration in Table 2), vapor pressure deficit, and annual incoming radiation (all correlations $r^2 = 0.80$, $P < 0.02$). These three environmental variables correlated highly with each other (r^2 0.62–0.83, P from 0.10 to 0.01).

Interestingly, the response to irrigation was strong in both the dry season (April to September) and the wet season (October to March; Fig. 5). Irrigation increased growth in the dry season by an average of 34% (9.5 Mg ha⁻¹ yr⁻¹ on an annual basis) across all sites,

and 23% during the wet season (8.0 Mg ha⁻¹ yr⁻¹ on an annual basis). Without irrigation, soil water supply apparently remained too low during at least some periods in the wet season to support maximum growth rates. The growth rate in irrigated treatments was also lower during the dry season than the wet season, with the 19% lower growth in the dry season matched by 19% lower incoming sunlight (data not shown). Dry-season growth in the non-irrigated plots was 27% lower than wet-season growth, reflecting the combined effects of lower incoming light and greater water stress.

Across sites, seasonal patterns of incoming light related well to seasonal growth when irrigation removed water stress. However, daily, seasonal, and annual growth were likely also influenced by vapor pressure deficit (VPD; see review by Whitehead and Beadle, 2004), as evidenced by differences in photosynthesis and water use on a daily basis (e.g. Hubbard et al., 2010), by differences in genotypes responses (Marrichi, 2009; Hubbard et al., 2010), by

Table 6

Mean annual increment of stemwood biomass at the end-of-rotation (6 years old) or at the last measurement by site (codes in Table 1) and treatment or factor (treatment codes from Table 4). Values inside parenthesis are standard errors of the mean; for the irrigation (N and I) and stand structure (H and U), values followed by the same letter do not differ at $P=0.05$ (see Table 5 for the other treatments comparisons).

Site (age)	Mean annual increment ($\text{Mg ha}^{-1} \text{yr}^{-1}$)									
	CNU	TNU	FNU	TIU	FIU	N	I	H	U	
ARA 6.0 years		18.3(0.5)	19.1(1.1)		28.1(1.2)	19.1(1.1) b	28.1(1.2) a	24.0(1.4)		28.1(1.2)
VER 6.0 years		29.7(1.5)	31.7(4.1)	36.7(1.3)	35.8(1.0)	30.7(2.0) b	36.2(0.8) a	26.7(1.6) b		32.7(1.4) a
IPB 6.0 years		25.6(1.1)	26.5(1.0)	34.3(1.5)	31.7(1.7)	26.1(0.7) b	33.0(1.1) a	25.8(1.1)		28.7(1.5)
SUZ 5.7 years		21.4(0.4)	21.5(0.3)		26.4(0.3)	21.5(0.3) b	26.4(0.3) a	22.0(1.2)		23.9(0.9)
CEN 5.3 years	21.3(1.8)	24.2(2.3)	24.9(2.1)	26.4(2.3)	26.2(2.8)	24.6(1.4)	26.3(1.7)			
VIP 4.8 years	14.4(3.0)	24.0(1.5)	24.0(3.2)	31.7(1.9)	28.0(3.7)	24.0(1.6) b	29.9(2.0) a			
VLM 4.5 years		20.8(1.3)	24.0(2.0)	37.3(2.6)	38.0(2.3)	22.4(1.2) b	37.6(1.6) a			
VCP 2.8 years	11.3(1.1)	15.9(0.1)	16.4(0.4)	21.7(0.5)	25.4(0.5)	16.1(0.2) b	23.5(0.7) a	21.9(0.4) b		25.4(0.5) a
Average	16.2(1.7)	22.6(0.8)	23.7(1.0)	31.3(1.3)	30.0(1.0)	23.5(0.7) b	30.6(0.8) a	24.4(0.7) b		28.0(0.8) a
Gain or loss	-28%	baseline	+4%	+32%	+27%	baseline	+30%	-13%		baseline

differences in growth among years with different average VPD (e.g. Stape et al., 2008), and the key role of VPD in predicting regional patterns of growth (e.g. Almeida et al., 2010).

3.3. Stand structure effect

Heterogeneous stand structure lowered growth by an average of 13% across the 5 sites that included this treatment (Table 6). The

stand structure effect was significant at all sites except ARA (two-tailed $P = 0.06$), as well as across all sites. The reasons for this effect remain unknown. All stems (within a site) were genetically identical, as were all supplies of resources. The interception of light did not differ at the plot scale (Ryan et al., 2010), so the lower growth in the heterogeneous treatment resulted from lower efficiency of light use rather than lower light interception. Binkley et al. (2010) examined light use efficiency at the scale

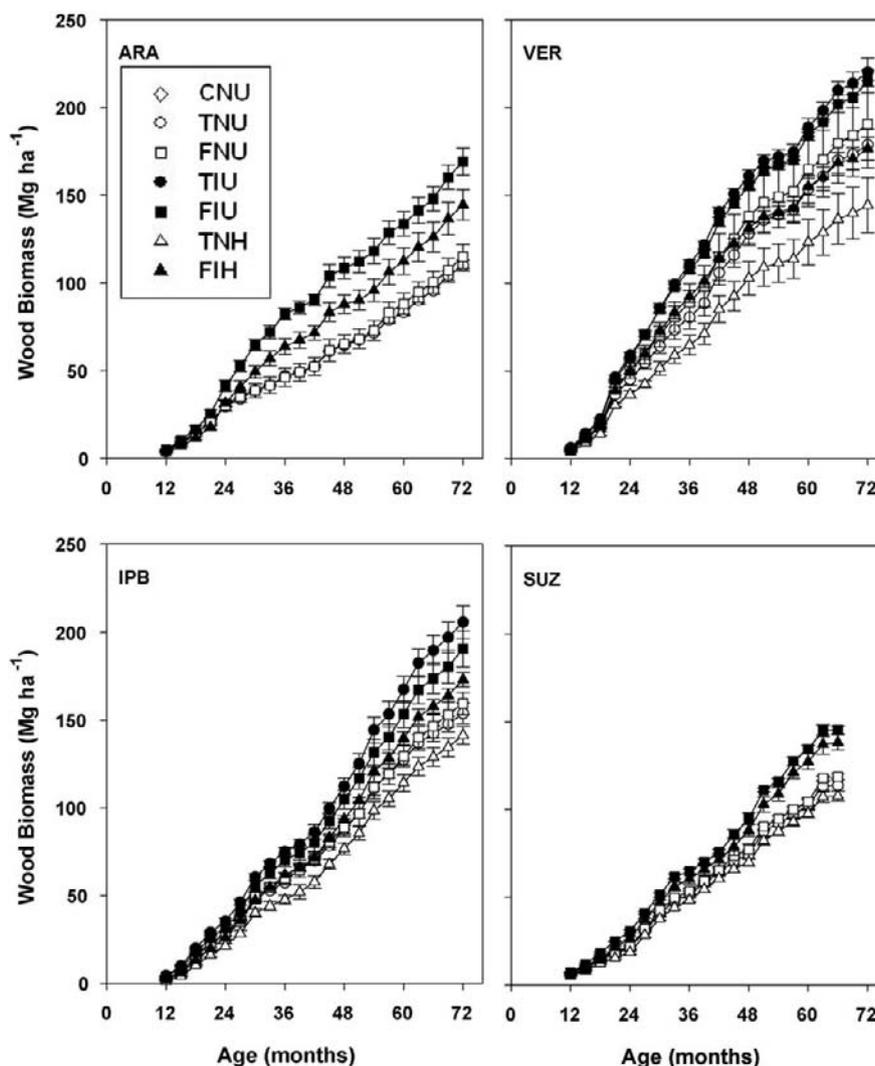


Fig. 3. Wood mass accumulation for each site (codes in Table 1) in relation to treatments (codes in Table 4). Error bars are standard errors of the means of 4 plots/site (3 for ARA). Open symbols indicate non-irrigated treatments, and closed symbols indicated irrigated treatments.

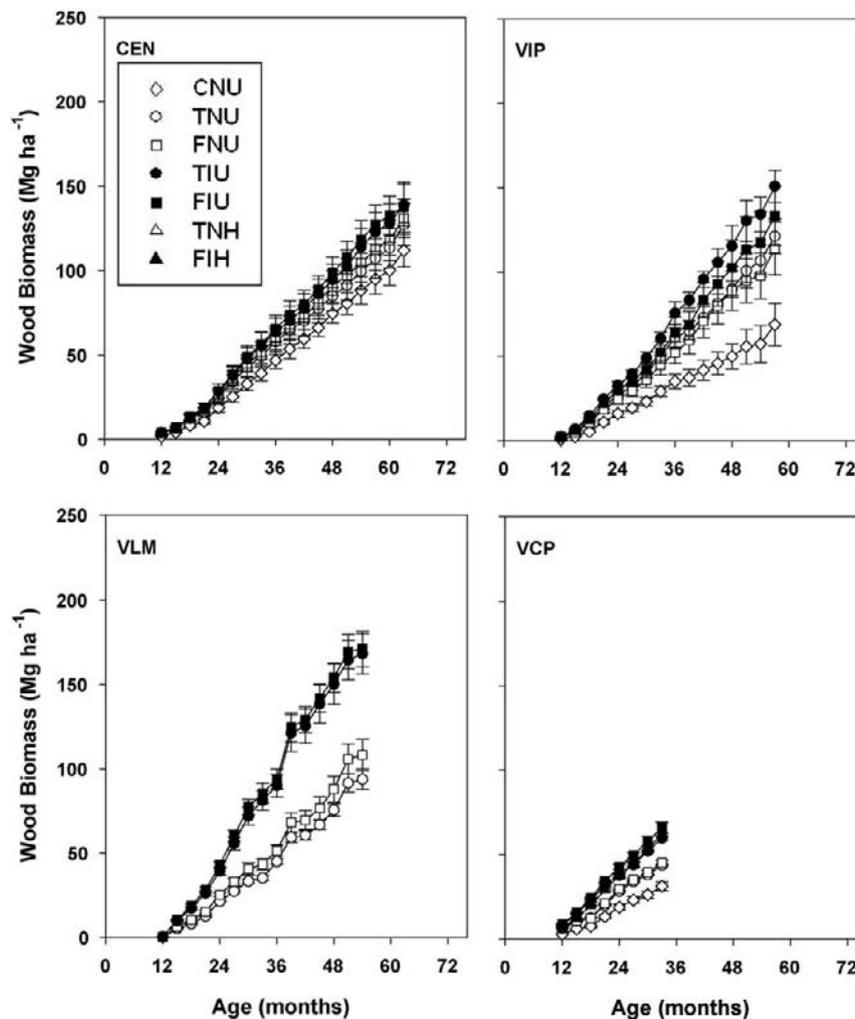


Fig. 3. (Continued).

of individual trees; non-dominant trees used light less efficiently than dominant trees, and this effect was accentuated by greater dominance in heterogeneous stands. The potential mechanisms behind these patterns clearly need to be examined with further research.

3.4. Culmination of increment

Across the three sites that spanned a full-rotation (ARA, IPB, VER), current annual increment culminated between age 2 and 4 (Fig. 6). The irrigated treatment showed a higher peak (about 45 Mg ha⁻¹ yr⁻¹ for the uniform treatment) than the non-irrigated treatment (about 33 Mg ha⁻¹ yr⁻¹). The peak CAI in irrigated plots (uniform treatment) was 13 Mg ha⁻¹ yr⁻¹ higher than late in the rotation, whereas the difference between peak CAI and late-rotation CAI was only 5 Mg ha⁻¹ yr⁻¹ without irrigation.

The decline in annual increment resulted largely from a decline in growth of non-dominant trees. The largest 20% of the trees (across treatments and sites) showed little or no decline in growth from mid-rotation to late-rotation, whereas growth dropped by about half for the 50th percentile trees (Binkley et al., 2010). The efficiency of light use also declined from mid-rotation to late-rotation, by 20–30% across all dominance classes. The sustained high growth rates of the dominant trees resulted from an increase in light capture and a decline in light use efficiency, leading to no net change in growth. Smaller trees declined in both light capture and light use efficiency.

We hypothesized that heterogeneous stand structure would lead to greater declines in production late in the rotation relative to uniform stands (Binkley et al., 2002; Binkley, 2004). However, the pattern of CAI over time was similar for both stand structure treatment, clearly refuting the hypothesis. High uniformity in stand structure did not moderate the decline in growth after the stands reached full leaf area.

4. Discussion

What is the potential productivity of Eucalyptus plantations in Brazil? This project led to several sorts of answers. Based on the three sites that reached a full-rotation, the potential stem wood productivity based on current operational silviculture (applied with close scrutiny under research conditions) averaged about 25 Mg ha⁻¹ yr⁻¹ (MAI for TNU treatment in Fig. 7), or about 51 m³ ha⁻¹ yr⁻¹. Removal of water limitation by irrigation raised the ceiling on potential productivity to about 32 Mg ha⁻¹ yr⁻¹ (about 65 m³ ha⁻¹ yr⁻¹). Operational-scale irrigation may be unlikely for most forests, but the gains from irrigation underscore the potential value of intensive management of site water balance (including site selection, site preparation, road planning and control of competing vegetation), and perhaps for genetic improvement objectives. These MAI figures include the first 18 months of the rotation before the trees fully occupied the sites with completely developed canopies and root systems, so the biological potential productivity for fully established trees would be a current

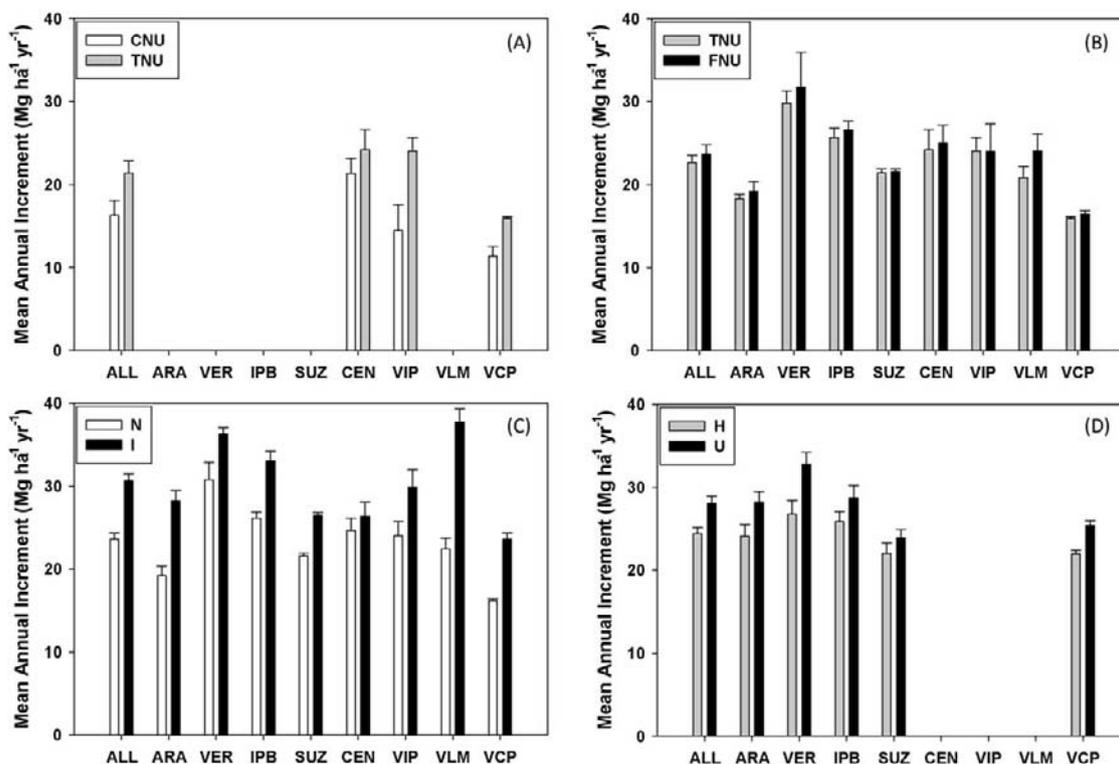


Fig. 4. Mean annual increment effect (for the entire period) for no fertilization versus traditional (current operational) fertilization without irrigation (A); traditional fertilization versus high fertilization without irrigation (B); the overall effect of irrigation (C); and the overall effect of stand structure (D). In all graphs, the first pair of bars presents the grand mean across sites (site codes in Table 1, treatment codes in Table 4). Error bars for the sites are the standard errors among plots within sites, and for the grand means the error bars are the standard variance among sites.

annual increment (ages 1.5–6.0 years) of about 38 Mg ha⁻¹ yr⁻¹ (77 m³ ha⁻¹ yr⁻¹). The biological productivity could also be considered for the portion of the year when climate conditions are most favorable, with low vapor pressure deficits and high sunlight. The current annual increment based on just the 6-month wet season reached about 42 Mg ha⁻¹ yr⁻¹ (83 m³ ha⁻¹ yr⁻¹). Higher rates of growth might be possible for some clones during some years on some sites, but the potential productivity estimates from this project probably represent the upper end of feasible rates for large areas for longer time periods. These potential levels can serve as a benchmark for comparison with yields obtained from

operational silviculture and the importance of operational auditing of quality control in precision silviculture (Goncalves et al., 2008).

The whole-rotation productivity for the treatments at the ARA, IPB and VER sites were predicted well by the mid-rotation results, so these patterns may support early decisions about the likely magnitude of full-rotation yields. Current annual increment from year 2 to 3 accounted for 85% of the variation in whole-rotation MAI across all treatments and sites. The MAI up to age 3 also predicted whole-rotation MAI ($r^2 = 0.68$), but not as well as current increment from year 2 to 3. The effects of increased water supply (TIU and FIU in relation to TNU) on biomass accumulation also related well to the increase in site index ($r^2 = 0.87$) pointing to the opportunity to increase the predictability of grow and yield empirical models for short-rotation forests by including some aspect of water supply into site index assessments (Maestri, 2003).

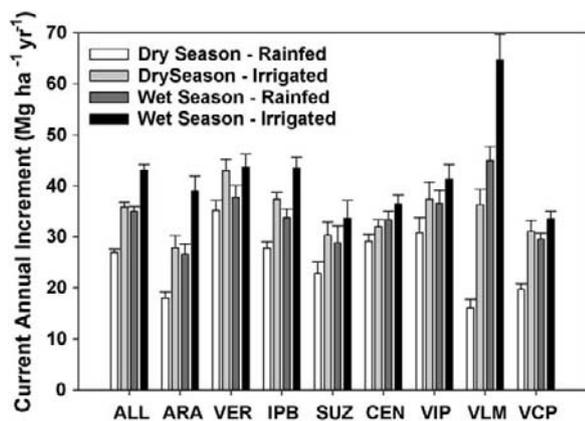


Fig. 5. Annualized rate of growth after canopy closure for comparing dry season and wet season patterns (site codes and season data in Table 1). With irrigation, wet-season growth was 19% greater than in the dry season (in response to higher vapor pressure deficit and lower incoming light). Without irrigation, the wet season grew 27% more than the dry season. Bars are standard errors of the mean within each site ($n = 4$ except ARA = 3); and for grand mean (all), bars are standard errors of the mean for 8 sites.

4.1. Nutrition

Eight sites clearly cannot encompass the full range of conditions across this broad region, so informed judgment is needed to extrapolate from our sample 8 sites to the region of Eucalyptus plantations in Brazil. For example, the growth response to very heavy fertilization at the VIP and IPB sites were no larger than the response to the traditional level of fertilization currently used by the companies (Table 6). Yet the average response among 258 “twin-plot” fertilization trials on these companies’ lands (at rates similar to those used at this site) was a 15–20% increase in wood growth (Stape et al., 2006; Ferreira and Stape, 2009). About 20% of the plots did not respond to fertilization in the twin-plot studies, so the VIP and IPB locations used in the BEPP Project would have fallen among this minority of non-responsive plots. Alternatively, fertilizer applications in operational treatments may be less precise than in research plots, so some of the apparent difference between the BEPP plots and the regionally representative

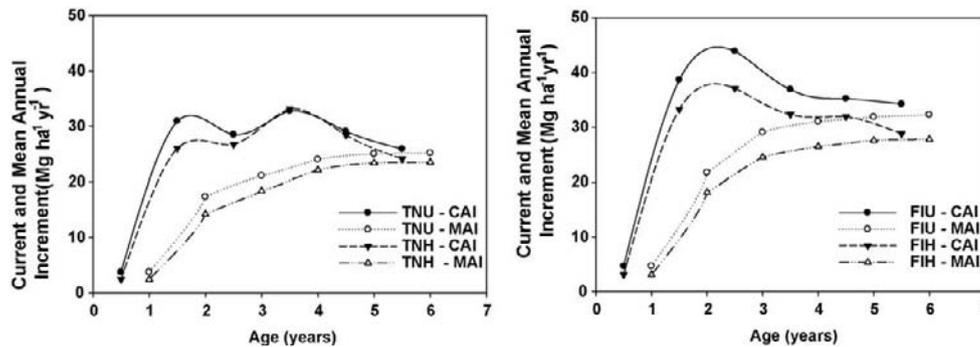


Fig. 6. Current and mean annual wood increments for the three sites (ARA, IPB, and VER) with a full-rotation of measurements. The expected decline after reaching full canopy development was apparent in all four treatments, but relatively minor. Contrary to expectation (Binkley et al., 2002; Binkley, 2004), uniform stands did not show less decline.

twin-plots might illustrate differences between operational stands and research plots. This is a key point, because the BEPP results indicated that current company prescriptions already attain a maximum fertilizer response, and perhaps lower rates would provide a similar response with a substantially lower cost. In contrast, the twin-plot results indicate current operations do not fully alleviate nutrient limitation on a majority of sites, so this discrepancy (an issue of real variation among sites, or in operational precision) needs to be examined.

4.2. Water stress

How did irrigation lead to increased wood growth? Irrigated plots showed higher levels of light use efficiency, expressed as wood growth per unit of light absorbed by the canopy (Ryan et al., 2010). This increased efficiency of light use reflected an increase in total gross primary production (GPP), an increase efficiency of light use (GPP per unit light absorbed), and a constant rate of total belowground carbon flux that allowed for increased production to be concentrated into wood growth. The higher efficiency of wood production per unit of light absorbed was consistent with the irrigation response of hardwood species (Cobb et al., 2008), for Eucalyptus in a mid-rotation study (Stape et al., 2008), and across a geographic rainfall gradient in Bahia (Stape et al., 2004b).

Increased wood growth in irrigated plots undoubtedly depended in part on greater water use, but we do not know the importance of any increase in water use efficiency across the sites. Late in the rotations at the ARA and VER sites, Hubbard et al. (2010)

estimated transpiration in trees and concluded that the growth response resulted only from increased water use (not increased efficiency of water use). This late-rotation pattern contrasts with the water use efficiency at mid-rotation at the Copener Florestal site, where the water balance for irrigated plots indicated higher efficiency of water use than in non-irrigated plots (Stape et al., 2008).

Simple water budgets that contrast rainfall and potential evapotranspiration at time scales of months (or years) would not capture the water limitations on Eucalyptus growth at our sites. Irrigation led to a 30% increase in stem growth, even though water balances (data not shown) indicated little if any water restriction on growth. Useful predictions of the effects of water supply on Eucalyptus growth probably require dynamic process-based models with relatively short time steps (daily or weekly; e.g. Almeida et al., 2004; Stape et al., 2004a).

Water supply is clearly critical to plantation productivity. Several irrigation studies have demonstrated strong relationships between water supply (and use) and wood production for Eucalyptus around the world, with stem growth responses of 15–35% (Linder, 1985; Madeira et al., 2002; Campion et al., 2006; Stape et al., 2008) or even higher under arid conditions (Hunter, 2001). The value of sites selected in the future for plantations in Brazil will depend strongly on a range of water-related issues, including rainfall, seasonality of rainfall and vapor pressure deficit, as well as soil water storage capacity (Almeida et al., 2004, 2010; Stape et al., 2004a). Adequate site preparation (such as subsoiling), water conservation, stocking and intensive control of competing vegetation may be particularly important in lowering water stress on trees in some sites, and environmental issues of total water consumption and efficiency of water use may shape silvicultural decisions as well as strategic planning by companies. Consistent with other studies (e.g. Madeira et al., 2002; Campion et al., 2006), we found no evidence of interactions between fertilization and irrigation, so issues of nutrition and water stress may be managed separately.

Explicit consideration of genotype differences in water acquisition and efficiency of use may be a valuable component of genetic improvement programs, with clear attention to interactions with silviculture and site factors. For example, it is not clear if higher growth rates would be achieved by genotypes that maximize water use, maximize efficiency of water use, or some optimal combination of both features (see Blum, 2008). These issues may be particularly important for the environmental impacts of intensive plantation forestry, especially for issues of stream-water yields in landscapes receiving less than 800 or 900 mm/yr of rainfall (Jackson et al., 2005; Little et al., 2009).

Water supply is also critical when rainfall varies among years, and the responses to these variations may differ substantially among clones. The next phase of the BEPP Project will examine

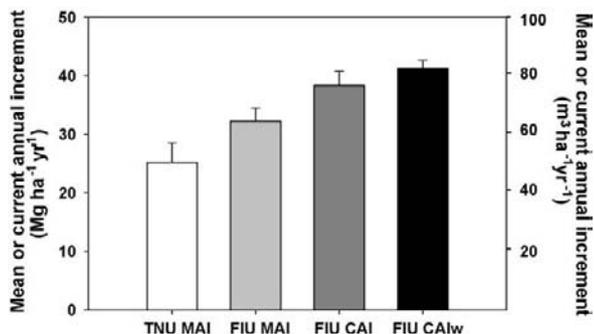


Fig. 7. Potential productivity may be characterized in various ways. These bars represent the growth for the three sites that completed a full-rotation (ARA, IPB, VER). The first bar is the mean annual increment for current operational silviculture (TNU MAI), and the second bar shows the rotation-long gains that may be obtained from irrigation (FIU MAI). The third bar represents average annual growth for the period once full canopies have developed (18 months, FIU CAI), and the final bar represents the biological maximum based on the full-canopy portion of the rotation, just for the wet, high-sunlight season (FIU CAIw).

these interactions with a variety of clones tested across the region, with rainfall exclusion treatments providing experimental manipulations of water supply within an expanded set of sites.

4.3. Stand structure

Operational irrigation is not widespread in plantation forestry, but all plantations develop a stand structure with low or high uniformity of tree sizes. The results of the BEPP Project indicate that uniformity in stand structure substantially influences wood growth. Indeed, much of the higher yield that typically occurs in clonal *Eucalyptus* plantations relative to seed-origin plantations may result from higher uniformity of tree sizes rather than genetic aspects (Binkley et al., 2002). The interactions of uniformity and genetics are probably complex. For example, Boyden et al. (2008) examined the competitive effects of neighbors on the growth of individual trees. A medium sized focal tree (75 kg wood mass) of clonal origin (surrounded by trees of the same clone) grew better than the same size tree from seed origin (surrounded by other seed-origin trees), when the overall size of neighbors offered little competition. As competition pressure increased with increasing size of neighboring trees, the growth of the clonal tree (with clonal neighbors) dropped below the level of the seed-origin tree (with seed-origin neighbors). A 50% increase in the competition index (based on the biomass of neighboring trees; see Boyden et al., 2008 for details) lowered the growth of the clonal tree by 20–30%, compared with a reduction of less than 10% in the seed-origin tree.

Silvicultural opportunities for promoting high uniformity in stand structure are clearly important, and more research is warranted on the mechanisms behind these responses as well as the interactions with genotypes. Dominant trees in the BEPP plantations showed higher light use efficiency than non-dominant trees (Binkley et al., 2010). It seems likely that this higher efficiency also reflects a pattern of allocation among tissues within trees, with higher allocation to wood growth relative to belowground by dominant trees. However, we have no information on belowground carbon flux on an individual tree basis, and other explanations remain possible.

The initial period of stand development shows low rates of stem growth as the canopy increases to a maximum. The period of time required for full canopy development may be reduced by increasing planting density, but the value of rapidly developing canopies may depend in part on overall site hydrology. Following harvesting and planting, soil water storage may be abnormally high as stand leaf area remains low; rapidly developing leaf area in high-density stands may begin to tap this stored water sooner than lower density stands. However, rapid reduction in stored soil water may not lead to higher MAI for the whole rotation, with intriguing potential interactions between the drawdown of stored soils water and genotype, silvicultural practices, stand density, and rate of canopy development.

The BEPP Project will continue for several more years, bringing all sites to the end of the first rotation. A second phase will examine a broader geographic range of sites, examining the effects of drought and genotypes. Future information will be posted at www.ipef.br/bepp, and then published in journals and other outlets.

Acknowledgements

The BEPP Project depended on the contributions of more than 100 people from 8 companies, and we thank them all for their contributions to the Project. The project was funded by Fibria, Veracel Celulose, International Paper, Suzano Papel e Celulose, CENIBRA, Vallourec-Mannesmann, and Copener Florestal. Otavio

Campoe, Cristiane de Lemos and Renato Meulman da Silva provided fundamental assistance in many aspects of the project. Cristian Montes provided insights about water use efficiency. J.L. Stape was sponsored by CNPq 306561/2007 and the ESALQ/University of São Paulo. M.G. Ryan's contribution to the Project was also supported in part by the USDA Forest Service.

References

- Almeida, A.C., Landsberg, J.J., Sands, P.J., 2004. Parameterisation of 3-PG model for fast-growing *Eucalyptus grandis* plantations. *For. Ecol. Manage.* 193, 179–195.
- Almeida, A.C., Siggins, A., Batista, T.R., Beadle, C., Fonseca, S., Loos, R., 2010. Mapping the effect of spatial and temporal variation in climate and soils on *Eucalyptus* plantation production with 3-PG, a process-based growth model. *For. Ecol. Manage.* 259, 1730–1740.
- Binkley, D., 2004. A hypothesis about the interaction of tree dominance and stand production through stand development. *For. Ecol. Manage.* 190, 265–271.
- Binkley, D., Stape, J.L., Ryan, M.G., Barnard, H., Fownes, J., 2002. Age-related decline in forest ecosystem growth: an individual-tree, stand-structure hypothesis. *Ecosystems* 5, 58–67.
- Binkley, D., Stape, J.L., Bauerle, W.L., Ryan, M.G., 2010. Explaining growth of individual trees: light interception and efficiency of light use by *Eucalyptus* at four sites in Brazil. *For. Ecol. Manage.* 259, 1704–1713.
- Blum, A., 2008. Effective use of water (EUW) and not water-use efficiency (WUE) is the target of crop yield improvement under drought stress. *Field Crops Res.* 112, 119–123.
- Boyden, S., Binkley, D., Stape, J.L., 2008. Competition among *Eucalyptus* trees depends on genetic variation and resource supply. *Ecology* 89, 2860–2867.
- Campion, J.L., Nkosana, M., Scholes, M.C., 2006. Biomass and N and P pools in above- and below-ground components of an irrigated and fertilized *Eucalyptus grandis* stand in South Africa. *Aust. For.* 69, 48–57.
- Cobb, W.R., Will, R.E., Daniels, R.F., Jacobson, M.A., 2008. Aboveground biomass and nitrogen in four short-rotation woody crop species growing with different water and nutrient availabilities. *For. Ecol. Manage.* 255, 4032–4039.
- Ferreira, J.M. de A., Stape, J.L., 2009. Productivity gains by fertilization in *Eucalyptus urophylla* clonal plantations across gradients in site and stand conditions. *Southern Forests* 71, 253–258.
- Goncalves, J.L.M., Stape, J.L., Laclau, J.-P., Bouillet, J.-P., Ranger, J., 2008. Assessing the effects of early silvicultural management on long-term site productivity of fast-growing eucalypt plantations: the Brazilian experience. *Southern Forests* 70, 105–118.
- Hubbard, R.M., Stape, J.L., Ryan, M.G., Almeida, A.C., Rojas, J., 2010. Effects of irrigation on water use and water use efficiency in two fast growing eucalyptus plantations. *For. Ecol. Manage.* 259, 1714–1721.
- Hunter, I., 2001. Above ground biomass and nutrient uptake of three tree species (*Eucalyptus camaldulensis*, *Eucalyptus grandis* and *Dalbergia sissoo*) as affected by irrigation and fertiliser, at 3 years of age, in southern India. *For. Ecol. Manage.* 144, 189–200.
- Jackson, R.B., Jobbagy, E.G., Avissar, R., Roy, S.B., Barrett, D.J., Cook, C.W., Farley, K.A., Le Maitre, D.C., McCarl, B.A., Murria, B.C., 2005. Trading water for carbon with biological carbon sequestration. *Science* 310, 1944–1947.
- Landsberg, J.J., Waring, R.H., 1997. A generalised model of forest productivity using simplified concepts of radiation-use efficiency, carbon balance and partitioning. *For. Ecol. Manage.* 95, 209–228.
- Linder, S., 1985. Potential and actual production of Australian forest stands. In: Landsberg, J.J., Parsons, W. (Eds.), *Research for Forest Management*. CSIRO, Melbourne, pp. 11–35.
- Little, C., Lara, A., McPhee, J., Urrutia, R., 2009. Revealing the impact of forest exotic plantations on water yield in large scale watersheds in South-Central Chile. *J. Hydrol.* 374, 162–170.
- Madeira, M.V., Fabião, A., Pereira, J.S., Araújo, M.C., Ribeiro, C., 2002. Changes in carbon stocks in *Eucalyptus globulus* Labill. plantations induced by different water and nutrient availability. *For. Ecol. Manage.* 171, 75–85.
- Maestri, R., 2003. Modelo de crescimento e produção implícito para povoamentos híbridos naturais de *Eucalyptus grandis* baseado em variáveis ambientais e do povoamento. Ph.D. thesis. Universidade Federal do Paraná, Curitiba, Brazil, 145 pp.
- Marrichi, A.H.C., 2009. Caracterização da capacidade fotossintética e da condutância estomática em sete clones comerciais de *Eucalyptus* e seus padrões de resposta ao déficit de pressão de vapor. MSc dissertation. ESALQ Universidade de São Paulo, Piracicaba, Brazil, 104 pp.
- Queiroz, R.D.S., Barrichelo, G., 2008. The Eucalypt: A Century in Brazil. Duratex S.A., São Paulo, 230 pp.
- Ryan, M.G., Binkley, D., Fownes, J., Giardina, C., Senock, R., 2004. An experimental test of the causes of age-related decline in forest growth. *Ecol. Monit.* 74, 393–414.
- Ryan, M.G., Stape, J.L., Binkley, D., Fonseca, S., Loos, R.A., Takahashi, E.N., Silva, C.R., Silva, S.R., Hakamada, R.E., Ferreira, J.M., Lima, A.M., Gava, J.L., Leite, F.P., Andrade, H.B., Alves, J.M., Silva, G.G.C., 2010. Factors controlling *Eucalyptus* productivity: how water availability and stand structure alter production and carbon allocation. *For. Ecol. Manage.* 259, 1695–1703.
- SAS Institute, 2000. SAS Software version 8.2. SAS Institute Inc., Cary, NC.

- Stape, J.L., Binkley, D., Ryan, M.G., 2004b. *Eucalyptus* production and the supply, use and the efficiency of use of water, light and nitrogen across a geographic gradient in Brazil. For. Ecol. Manage. 193, 17–31.
- Stape, J.L., Binkley, D., Ryan, M.G., 2008. Production and carbon allocation in a clonal *Eucalyptus* plantation with water and nutrient manipulations. For. Ecol. Manage. 255, 920–930.
- Stape, J.L., Ryan, M.G., Binkley, D., 2004a. Testing the utility of the 3-PG model for growth of *Eucalyptus grandis* × *urophylla* with natural and manipulated supplies of water and nutrients. For. Ecol. Manage. 193, 219–234.
- Stape, J.L., Binkley, D., Jacob, W.S., Takahashi, E.N., 2006. A twin-plot approach to determine nutrient limitation and potential productivity in *Eucalyptus* plantations at landscape scales in Brazil. For. Ecol. Manage. 223, 358–362.
- Thorntwaite, C.W., Mather, J.R., 1957. Instructions and tables for computing potential evapotranspiration and the water balance. Publ. Climat. 10, 185–311.
- Whitehead, D., Beadle, C.L., 2004. Physiological regulation of productivity and water use in *Eucalyptus*: a review. For. Ecol. Manage. 193, 113–140.